

THE SKELETON OF THE MAMMAL-LIKE REPTILE *CISTECEPHALUS*
WITH EVIDENCE FOR A FOSSORIAL MODE OF LIFE

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(With 20 figures)

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ABSTRACT

A full description of the skeleton of *Cistecephalus*, based on a number of specimens, is given. A skeletal reconstruction shows that *Cistecephalus* was probably the most aberrant member of the infraorder Dicynodontia, and comparison with living animals suggests that the osteological modifications of, in particular, the shoulder girdle and forelimb represent adaptations to powerful and frequent digging activities.

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INTRODUCTION

The cranial morphology of the Upper Permian dicynodont *Cistecephalus* has been made well known through a succession of papers following Owen's original description of the genus in 1876. Chief among these are those of Seeley (1894), Broom (1932, 1948), Broili & Schröder (1935), Brink (1950, 1952), Keyser (1973) and Cluver (1974). As details of the skull structure were established, it became clear that *Cistecephalus* was a highly specialized animal showing a number of fundamental departures from the usual dicynodont condition. As these specializations must represent adaptations to a specific way of life, *Cistecephalus* has been the subject of some speculation by a number

of authors. Aquatic habits were proposed by Broom (1948) and Brink (1950), but the latter author later (Brink 1952) maintained that the structure of the manus indicated adaptations to digging activities. Keyser (1973) thought that the orientation of the orbits and possible opposability of digits of the manus pointed to commitments to arboreality, but included digging activities as part of the animal's general way of life. Cluver (1974) compared the skull of *Cistecephalus* with that of the related *Kawingasaurus*, for which genus Cox (1972) had produced convincing evidence of powerful digging or fossorial habits, and also with skulls in living and extinct fossorial mammal groups, and concluded that *Cistecephalus* was in all likelihood an accomplished digger.

Since only tantalizingly little of the cistecephalid postcranial skeleton has been described in the literature (Brink 1952, Keyser 1973, Von Huene 1942, Cox 1972), it seemed worth while to investigate available material of the genus in order to determine whether the peculiarities in the cranial structure are matched by specializations in the axial and appendicular parts of the skeleton. As a result of this exercise, it has been possible to establish a complete reconstruction of the cistecephalid skeleton, which shows that the living animal was probably the most specialized and aberrant member of the infraorder Dicynodontia, in itself a highly modified division of the order Therapsida.

Studies on the postcranial skeleton of Permian dicynodonts are regrettably few; in this investigation use was made chiefly of the accounts by Watson (1960), Cox (1959, 1972) and Boonstra (1966).

MATERIAL

SAM-10665. *Cistecephalus* sp. Ou Plaas, Murraysburg, Cape Province. The skull, complete but slightly compressed dorsoventrally, has been fully prepared. The lower jaw, lacking the posterior part of the right ramus, has been separated from the skull and also fully prepared.

BPI 4086. *Cistecephalus* sp. Bloukop, Roggevelei boundary between Richmond and Victoria West, Cape Province. An almost complete skeleton, showing the skull and lower jaw, the vertebral column and ribs, the right scapula, humerus, radius and partial manus, a complete left hind limb and the right femur and distal ends of the tibia and fibula. The atlas and last caudal vertebrae are absent.

BPI 696. *Cistecephalus* sp. Aasvogelkrans, Murraysburg, Cape Province. A skull and lower jaw with associated but largely disarticulated postcranial skeleton. The right scapula, left humerus and ulna and partial left manus are well displayed, as well as the pelvic girdle, sacral and caudal vertebrae.

BPI 2915. *Cistecephalus* sp. Beeldhouersfontein, Murraysburg, Cape Province. A skull and lower jaw with cervical vertebrae, pectoral girdle and complete left forelimb and manus.

BPI 506. *Cistecephalus* sp. Towerwater, Murraysburg, Cape Province. A skull and lower jaw with anterior vertebrae, a complete pectoral girdle and a good left humerus.

BPI 2450. *Cistecephalus* sp. Klipplaat, Murraysburg, Cape Province. A skull and partial lower jaw with isolated ribs and the right half of the pelvic girdle.

BPI 4120. *Cistecephalus* sp. Modderfontein, Victoria West, Cape Province. Skull and anterior part of vertebral column, pectoral girdle and articulated forelimbs.

RC 298. *Cistecephalus* sp. Tweefontein, Graaff-Reinet, Cape Province. Good skull and lower jaw with anterior part of vertebral column and ribs, a nearly complete pectoral girdle and a good left humerus with the proximal part of the ulna in articulation.

BPI 2124. *Cistecephalus* sp. Kraaifontein, Murraysburg. Skull and lower jaw with pectoral girdle and right and left forelimbs in near-natural articulation. Left manus seen in ventral view.

GS K224. *Cistecephalus* sp. Steilkranz, New Bethesda. Skull and lower jaw with articulated anterior part of postcranial skeleton. Manus of left and right sides seen in ventral view.

SAM-11114. *Oudenodon* sp. Melton Wold, Victoria West. Skull, lower jaw, pectoral girdle and left and right forelimbs.

All specimens are from Upper Permian, *Cistecephalus* zone localities.

THE SKELETON OF *CISTECEPHALUS*

Skull and lower jaw

The *Cistecephalus* skull and lower jaw have been fully described by Keyser (1973) and need not be considered in detail here. Some features of functional significance may, however, be mentioned. As suggested by Cluver (1974), the broad intertemporal region and rounded occiput may reflect forward extension and hence increased size of the neck and shoulder musculature, such as is found in many burrowing mammals. The basicranial region is strengthened by a meeting in the ventral midline between the pterygoids, vomer and the base of the presphenoid, with the obliteration of the interpterygoidal vacuity.

The lower jaw is short, deep and robust. The dentary symphysis is extended as a sharp transverse blade which met the premaxillary part of the secondary palate during mastication. This scoop-like anterior edge of the lower jaw is narrower than the secondary palate, and it is likely that the lower jaw could be moved laterally across the secondary palate while crushing food in the mouth. The short lower jaw did not meet the blunt anterior edge of the premaxilla at any time during the masticatory cycle.

In Figure 20 skull details are derived from SAM-10665 and BPI 4086. Detailed drawings of cistecephalid skulls have been published by Keyser (1973) and Cluver (1974).

Vertebral column

In RC 298 the atlas, axis and succeeding 6 cervical vertebrae are preserved in natural or near-natural articulation (Figs 1-2). The right half of the atlas neural arch lies slightly displaced upon the odontoid process of the axis, and

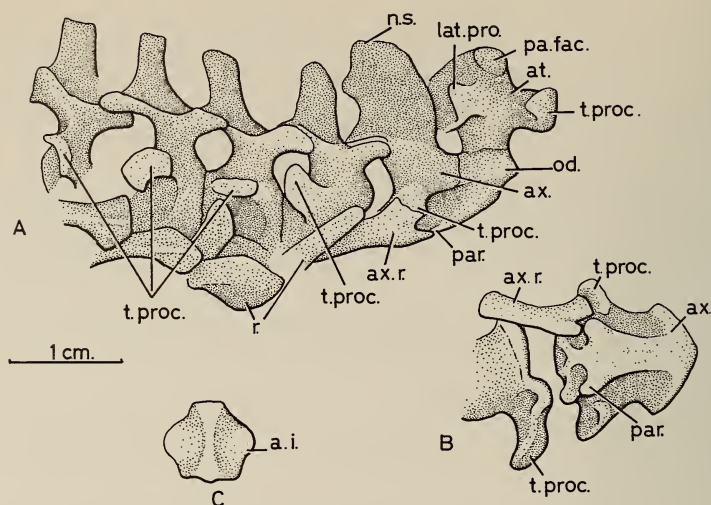


Fig. 1. *Cistecephalus* sp. RC 298. A. Cervical vertebrae in right lateral view. B. Axis and 3rd cervical vertebra in ventral view. C. Atlas intercentrum in ventral view.

carries a strong anteroposteriorly elongated transverse process. The facet for the proatlas is situated on a distinct raised platform. The body of the atlas arch carries a large posteromedially facing facet that articulates with the odontoid process, and an anteromedially facing facet that meets the occipital condyle. An isolated atlas intercentrum is present. The element is transversely expanded and carries a ventral longitudinal crest. Little can be seen of the articulatory facets for the odontoid and occipital condyle, but it appears that the bone is flatter than that of *Lystrosaurus* (Cluver 1971).

The axis is well preserved. The neural arch is indistinguishably fused to the centrum, and bears a broad spine, higher than those of the succeeding vertebrae. The postzygapophysis is tightly articulated with the prezygapophysis of the next vertebra, but the prezygapophyseal region is damaged, evidently as a result of the displacement of the atlas. The centrum of the axis carries a distinct transverse process and is apparently fused with the odontoid element. There is a smaller process, the parapophysis, low down on the centrum directly beneath the transverse process, serving for the articulation of the capitulum of a short but stout axial rib.

Six vertebrae are preserved in articulated position behind the axis, the last two incompletely exposed. The three immediately behind the axis have narrower spines than the fourth, and could represent true cervicals. Including atlas and axis, this would mean a total of five cervical vertebrae in the column. The third cervical carries a long, backwardly and dorsally directed transverse process, much more prominent than those of the axis or the succeeding vertebrae; the transverse processes of the last two cervicals are directed laterally and

only slightly posteriorly. The zygapophyses of the cervicals, particularly the last two, are set close to the neural spine and are tightly interlocked. In what is regarded as the first dorsal vertebra, the transverse process is short and excavated posteriorly, so that in lateral view the distal surface of the process is arcuate in outline.

In BPI 4086 the vertebral column is complete except for the atlas and the most posterior tail vertebrae. In this specimen, too, a total of five cervicals can be recognized. The first three cervicals, including the axis, are articulated, but

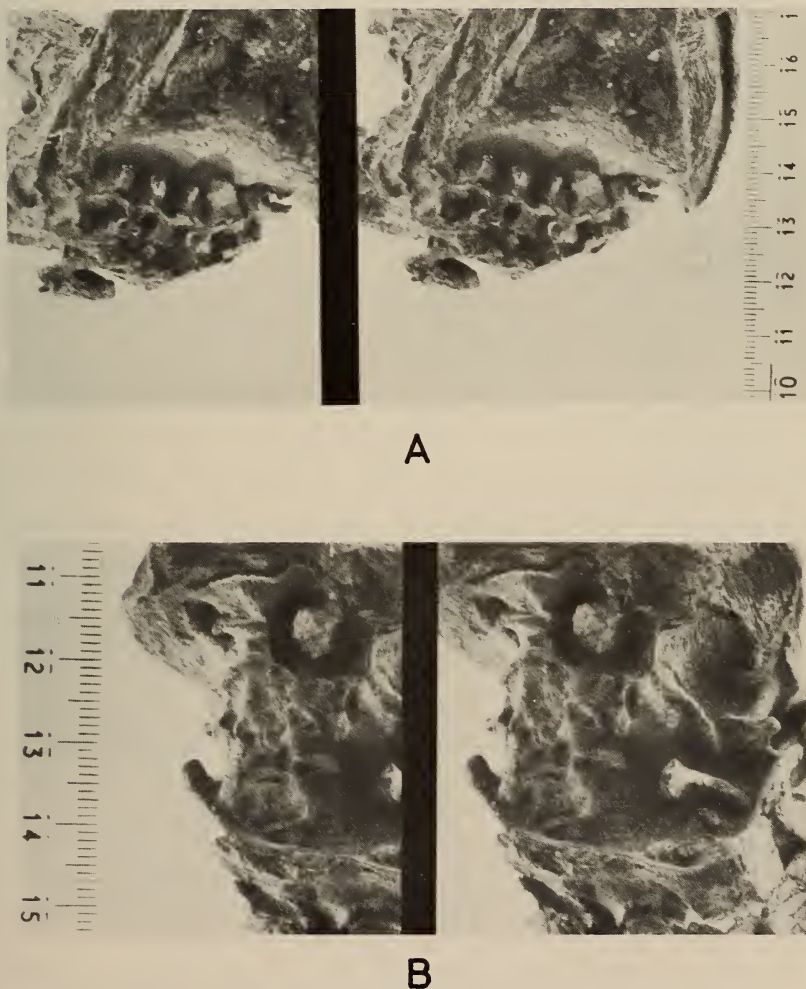


Fig. 2. *Cistecephalus* sp. RC 298. Stereophotographs of anterior cervical vertebrae. A. Right lateral view. B. Ventral view.

the fourth and fifth in the row are loose from each other and from the sixth, from which point the column is again fully articulated. The fourth in the row (fifth cervical) is more complete than the anterior vertebrae; the spine appears narrower than that of the succeeding vertebra, which differs, too, in the stouter transverse process carried higher on the neural arch. This latter vertebra can be regarded as the first dorsal (see p. 219). A total of twenty-five dorsals is present. All are damaged to some extent, and the twenty-first and twenty-second dorsals have become separated from each other. As far as can be made out, the dorsals have broader neural spines than the cervicals, and in some instances this width becomes extreme. The twenty-second dorsal has a very broad anteroposteriorly inflated spine; the adjoining vertebrae are too damaged to give any indication of the breadth of their spines. In all the vertebrae, including the cervicals, the zygapophyses articulate at steep angles to the horizontal.

Three sacral vertebrae are present in BPI 4086, each apparently indistinguishably fused to its pair of ribs (Fig. 16A). The first sacral rib is very deep, as is the second, but the third is less strongly developed. All three sacral vertebrae are damaged and many details are lacking, but it seems that the spine of the second slopes back to a much greater degree than does that of the last dorsal.

In BPI 696 the two halves of the pelvis are in near-natural position relative to each other and sacral and caudal vertebrae are preserved. The first sacral vertebra is partially exposed and its right rib is seen in anteroventral view. The rib is short and wide distally and is not fused to the vertebra, which it meets close to the body of the centrum. The centra of three vertebrae are visible in ventral view behind the first sacral; the last of these is that of the first caudal. In this specimen the remaining caudal vertebrae have folded over to lie upon the dorsal spines of the sacral vertebrae, obscuring them from view. Only the ventral surfaces of the centra, and in some cases the ribs, of the caudal vertebrae are visible. A total of fifteen caudals is present, the last being a mere fleck of bone and it seems likely that this represents a complete or near-complete series, although it is possible that members of the series may be missing at the point of dislocation from the sacral series.

In BPI 4086 four caudal vertebrae, all damaged and the last very incomplete, are present. The second caudal has a fairly long laterally directed rib.

As far as can be seen, the zygapophyses of all vertebrae examined meet each other at steep angles to the horizontal, and it is likely that only dorso-ventral flexure or rotation between vertebrae could have been possible, even in the neck region. No horizontal or near-horizontal articulations are present anywhere in the column.

Ribs

The anterior ribs are best seen in RC 298. There is no indication of an atlantal rib, but a short, stout and double-headed axis rib is present (Fig. 1). The second rib present, that of the third cervical, is poorly preserved and it is

not possible to determine whether a double head was present; there is, however, no clear parapophysis for attachment of the capitulum, as in the axis. In the fourth cervical a short and relatively slender double-headed rib is present. In the fifth cervical the rib is incomplete but longer than that of the fourth. The capitulum and tuberculum lie close to each other and are separated by a very shallow notch. The next two ribs are almost complete, and lie crossed over each other with the ventral ends meeting the side of the sternum in what appears to be a natural association. The sixth vertebra carries the anterior of these two ribs and can be regarded as the first dorsal, an identification supported by characters of the vertebrae themselves (see p. 218). The head of the first dorsal rib is incomplete, but that of the second dorsal is wide and a separate capitulum and tuberculum cannot be made out. It seems likely (see below) that in this specimen at least three ribs are attached to the sternum.

In BPI 4086 ribs are preserved from the first dorsal vertebra to the twenty-fourth dorsal vertebra. Ribs are very short in the posterior region and are longest between the sixth and eleventh dorsal, but it should be noted that none of the ribs is absolutely complete. As shown above, the second caudal vertebra carries a simple, laterally directed rib. In BPI 696 the first three caudals in the dislocated portion of the row have short, slender ribs; there is no sign of haemal arches in this series, and the base of the tail was probably clearly demarcated from the rest of the body.

Pectoral girdle and forelimb

In RC 298 there is an almost complete left scapula, procoracoid and coracoid, a complete clavicle on both sides, an interclavicle and a sternum (Figs 3–5). The left humerus is present in natural articulation with the glenoid, but is damaged proximo-anteriorly. The olecranon portion of the ulna is preserved in contact with the left humerus. On the right side the clavicle articulates with the acromian process of the scapula, which is complete below the level of this process. The proximal part of the humerus is preserved in position in the glenoid cavity. A complete coracoidal plate is also present, but is slightly obscured by the overlying clavicle.

The scapula is a long, relatively slender bone. The acromian process, situated low down close to the level of the glenoid, is a continuation of the anterior edge of the scapula blade and is formed more by an excavation of the anterior edge of the blade than by a separate bony projection (see Watson (1960) fig. 12). The upper half of the scapular blade is bent back relative to the lower half and the bone can thus be divided into an acromian section and an upper section, lying at about 25° to each other. Below the acromian process the base of the scapula is turned sharply inwards to meet the procoracoid. The glenoid is a well-defined hollow bounded by a sharp, flared rim, and faces laterally rather than posterolaterally as in other dicynodonts (Watson 1960).

The procoracoid/coracoid plate is more complete on the right side, but is partially obscured by the clavicle. There are no clear boundaries between the

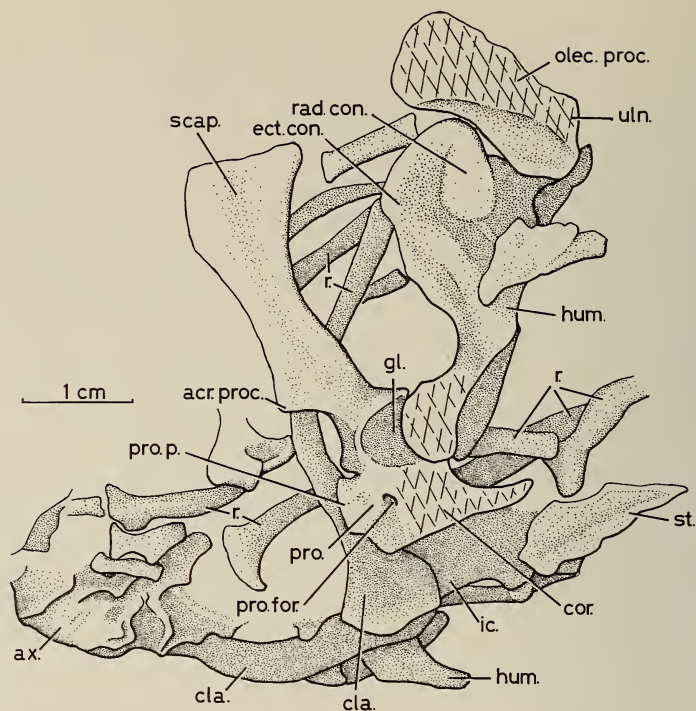


Fig. 3. *Cistecephalus* sp. RC 298. Semi-articulated pectoral girdle in left lateral view.

two elements making up the plate, but a ridge running forward from the rear of the glenoid cavity may indicate a large coracoid, forming most of the ventral part of the glenoid cavity. The anterior edge of the procoracoid is expanded to form a fairly robust process which abutted against the clavicle of its side. A procoracoid foramen is present half-way between the ventral limit of the anterior procoracoid process and the ventral rim of the glenoid cavity.

The clavicle is a fairly stout bone with a wide contact with the inner surface of the scapula at the level of the acromion process, and a broad ventral meeting with the clavicle of the other side in the ventral midline. Along the midline each clavicle is dorsoventrally expanded, so that the pair meet over a wide area. This connection seems to have been a strong one and is preserved in most specimens. The median plate formed by the two clavicles in the ventral midline is overlain by the front of the interclavicle, less robust in comparison. Half-way down the posterolateral surface of its shaft the clavicle carries a recess, bounded laterally by a thin crest of bone, which in size and position is suited for articulation with the anterior procoracoid process. This articulation would have served to strengthen the connection between clavicle and scapulocoracoid, and prevent forward and inward displacement of the scapulocoracoid resulting from forces at the glenoid.

The partially exposed interclavicle is seen as a flat, rectangular sheet with its anterior end obscured by the meeting between the clavicles, and its posterior end lying above the sternum. The sternum is fully exposed and most of its structure can be made out. It is wide and flat-edged anteriorly and tapers posteriorly to a fairly narrow median spine. A prominent ventral median crest

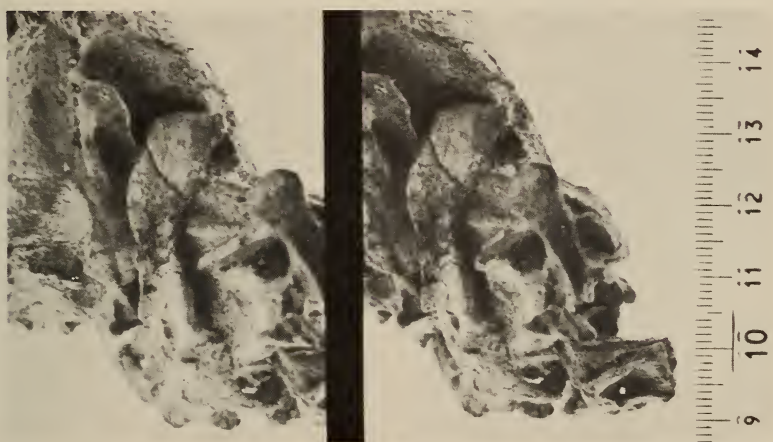
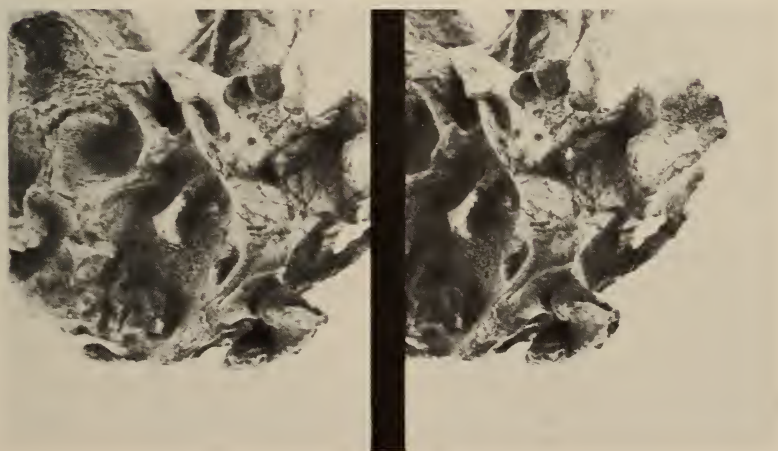
**A****B**

Fig. 4. *Cistecephalus* sp. RC 298. Stereophotographs. A. Left scapulocoracoid in lateral view. B. Pectoral girdle in ventral view.

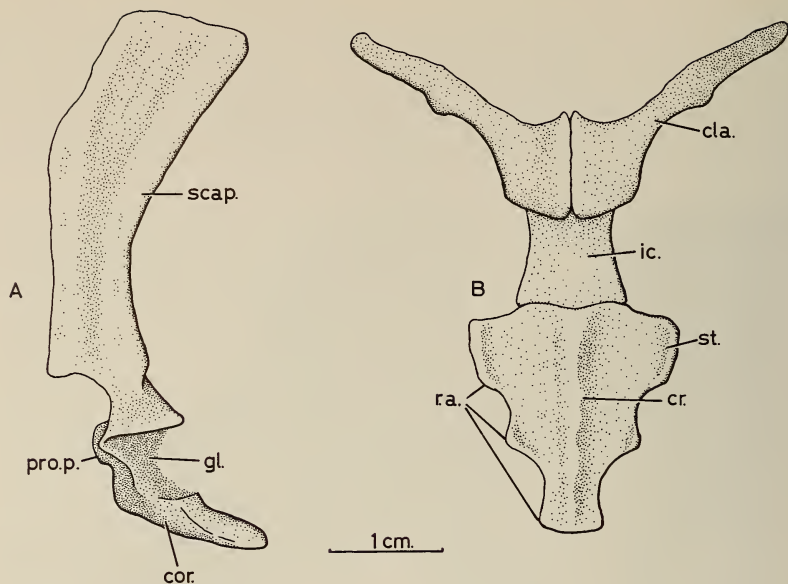


Fig. 5. *Cistecephalus* sp. RC 298. A. Left scapulocoracoid in lateral view. B. Pectoral girdle in ventral view.

runs the length of the bone. On each side three processes for the attachment of ribs can be made out, one behind the anterolateral corner of the bone, one half-way down the side and one on the posterolateral corner. On the right side two ribs are in near natural articulation with the two most anterior processes. The distances separating the three processes are approximately the same.

Several additional specimens show further details of the pectoral girdle. In BPI 2915 a good scapula, with cleithrum, is present, differing from that in RC 298 in that it extends straight dorsally without a posterior twist in the dorsal half. On the left side the coracoid and procoracoid have become detached from the scapula, and the suture between the two ventral elements can be seen running vertically and transversely through the middle of the ventral part of the glenoid. The procoracoid foramen is situated in the centre of the procoracoid, well away from the glenoid cavity. In BPI 696 the right scapula, of which the dorsal part is damaged, shows the acromian region well. The procoracoid is present, though apparently incomplete, and where the two bones have moved slightly apart it can be seen that the scapula extends ventrally for a considerable distance on the inside of the procoracoid. In BPI 4086 and BPI 2124 the scapula is bent towards the rear as in RC 298.

In BPI 2915 a distinct cleithrum is present, and this appears to have been the case in the other specimens as well. Von Huene (1942) described this element in material later referred to *Kawingasaurus* by Cox (1972).

In GS K224 (Fig. 12A) the interclavicle is not completely preserved and the sternum has apparently been eroded away. Seen in the midline above where the sternum would have lain are the bases of the coracoids, meeting over the anterior parts of their inner surfaces in what appears to be a natural relationship; all the remaining postcranial elements in this specimen are in natural articulation with each other. In BPI 2915 a similar meeting of the coracoids in the midline, over the rear of the interclavicle and the front of the sternum, seems likely.

The best humerus is that of the right side in BPI 4086 (Figs 7-8), but the bone is also well preserved in BPI 506 (Fig. 9) and BPI 696 (Fig. 10). The bone is almost as broad as it is long, and is characterized by greatly enlarged processes serving for muscle attachment. There is a clearly demarcated head (*caput humeri*), forming the most proximal corner of the bone and facing dorsally as a prominent, slightly rounded condyle. The head is especially strongly developed in BPI 506. Behind this the posterior corner of the humerus is extended as a powerful posteromedial process, which consists of a neck portion and an expanded terminal portion. In front of the humeral head the inner, anterior edge of the bone is drawn forward as a broad, thin deltopectoral crest, with a thickened leading edge.

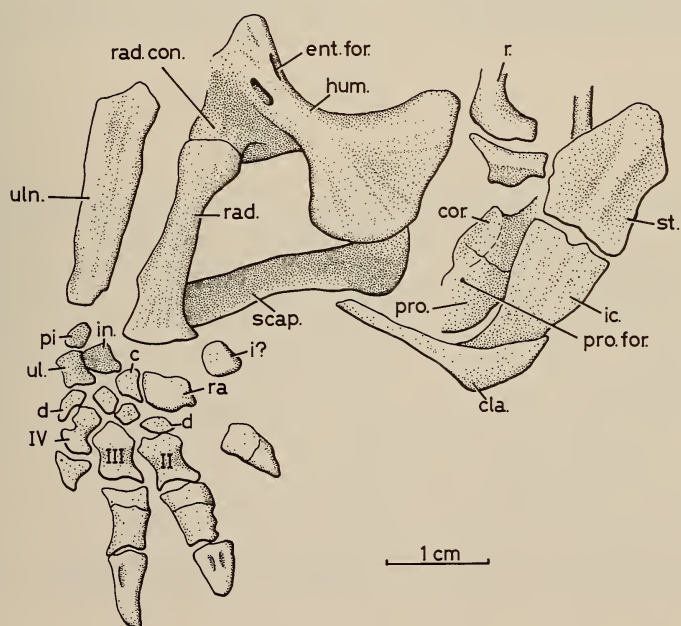


Fig. 6. *Cistecephalus* sp. BPI 2915. Partial pectoral girdle and left forelimb. Manus seen in ventral view.

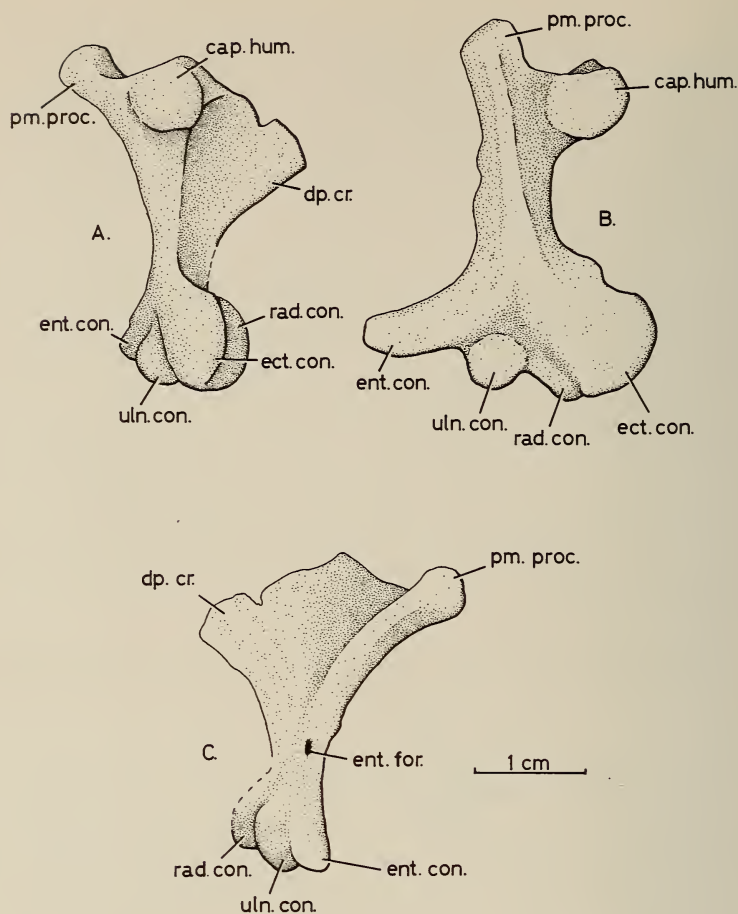


Fig. 7. *Cistecephalus* sp. BPI 4086. Right humerus. A. Dorsal view. B. Posterior view. C. Ventral view.

The proximal part of the humerus is convex dorsally and concave ventrally. The distal half is twisted so that the plane in which the distal edge lies is at right angles to the plane in which the deltopectoral crest and posteromedial process lie. In this way, when the proximal part of the humerus is brought to lie in the horizontal plane, the articular surfaces for the radius and ulna on the distal edge face forward and laterally. With the distal edge in the horizontal plane, the most anterior part is formed by the broad ectepicondyle. A thin crest leads medially from the ectepicondyle to merge with the body of the humerus near the waist of the bone. Below and behind the ectepicondyle is a prominent, rounded condyle for the radius, separated from the ectepicondyle by a distinct groove. Behind this is a smaller but equally distinct condyle for the ulna; the

distal edge of the humerus is thinner in this region, and the ulnar condyle stands clear of both the dorsal and ventral surfaces of the bone, while on the dorsal surface there is a slight depression medial to the condyle. This depression is deepest in BPI 506, where the condyles are very powerfully developed. Posterior to the ulnar condyle the humerus is extended as a long, relatively slender entepicondyle. At the base of this process, near the waist of the bone, the humerus is pierced by the entepicondylar foramen.

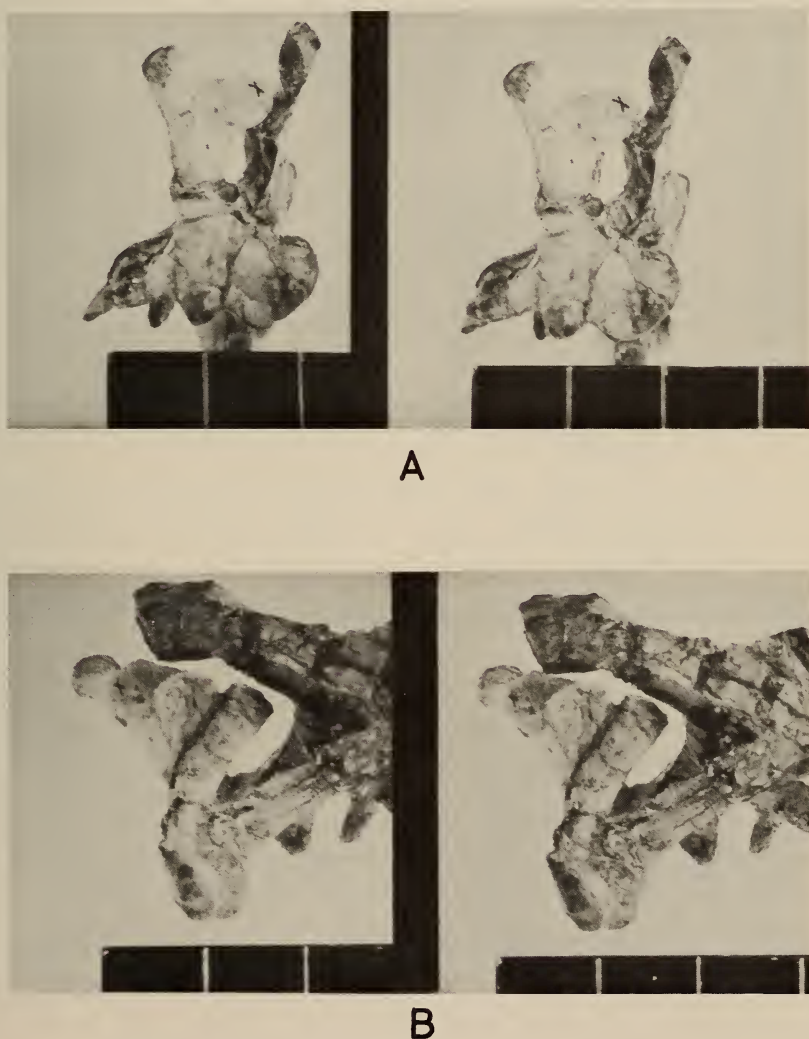


Fig. 8. *Cistecephalus* sp. BPI 4086. Stereophotographs of right humerus.
A. Posterior view. B. Dorsal view.

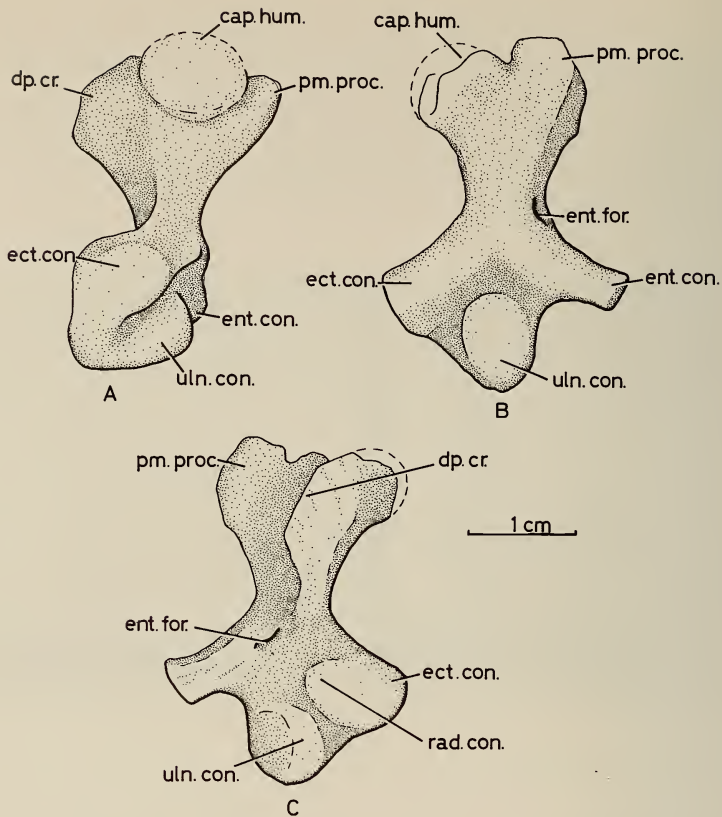


Fig. 9. *Cistecephalus* sp. BPI 506. Left humerus. A. Dorsal view. B. Posterior view. C. Ventral view.

The radius is well preserved in BPI 2915 (Fig. 6) and BPI 2124 (Fig. 11). The length of the bone in BPI 4086 is equal to that of the humerus between the humeral head and the outside surface of the radial condyle. The ulna is fairly robust, widened proximally for the meeting with the humerus and flared distally to meet the bones of the carpus over a fairly broad area. A posterior crest on the distal end gives the bone a triangular cross-section where it meets the carpus.

The ulna (Figs 6, 10–11) is present in BPI 2915, BPI 696 and BPI 2124. It is characterized by a wide and powerful olecranon process extending up above a notch for articulation with the ulnar condyle on the humerus. The shaft of the ulna is slender, and the distal extremity is rounded in section and narrower than that of the radius. On the posterior surface a deep groove extends down the shaft from the level of the articulatory facet for the humerus.

The carpus is best seen in BPI 2915 (Figs 6, 13), where the ventral surfaces of the bones are exposed. The radius and ulna are separated from the carpus

by a slight gap, within which three small bones lie alongside the ulna. The one nearest the ulna can be regarded as a pisiform, drawn medially during the pulling apart of the wrist, while of the other two the lateral one probably represents an ulnare, and the medial element the intermedium. The remainder of the carpus is still undisturbed and the bones can be identified with a fair amount of certainty. There are a large medial radiale and a centrale, followed distally by a row of four distalia. In BPI 2124, the specimen described by Brink (1952), an ulnare, an intermedium and a large radiale are present, as well as four, possibly five, distalia (Fig. 11). A centrale is also present. The doubtful fifth distal is the most median one, which may actually be part of the radiale. The middle distale is smaller than figured by Brink, who mistook part of the third metacarpal as being part of it. The most lateral distale, behind the fourth

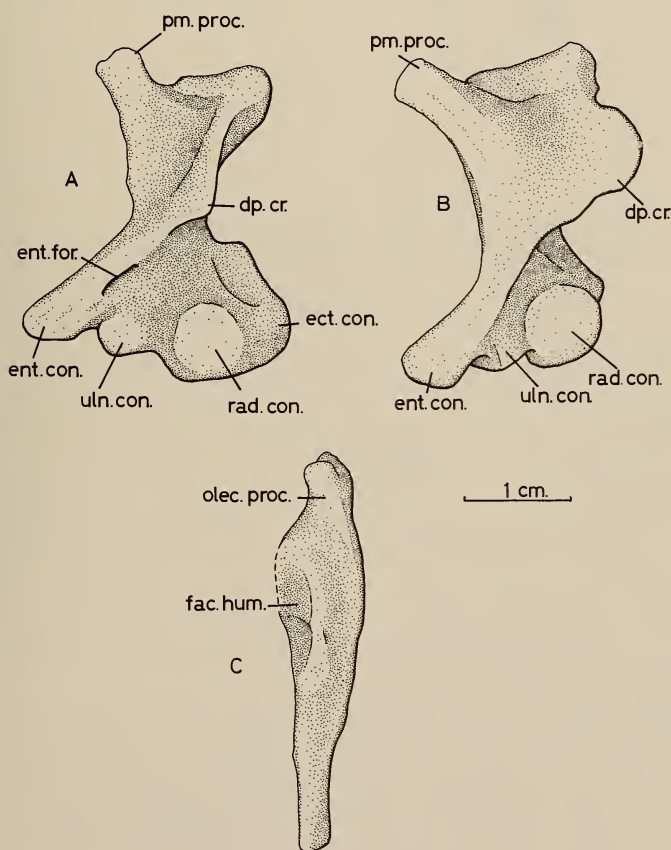


Fig. 10. *Cistecephalus* sp. BPI 696. Left humerus. A. Anteroventral view. B. Ventral view. C. Left ulna in anterior view.

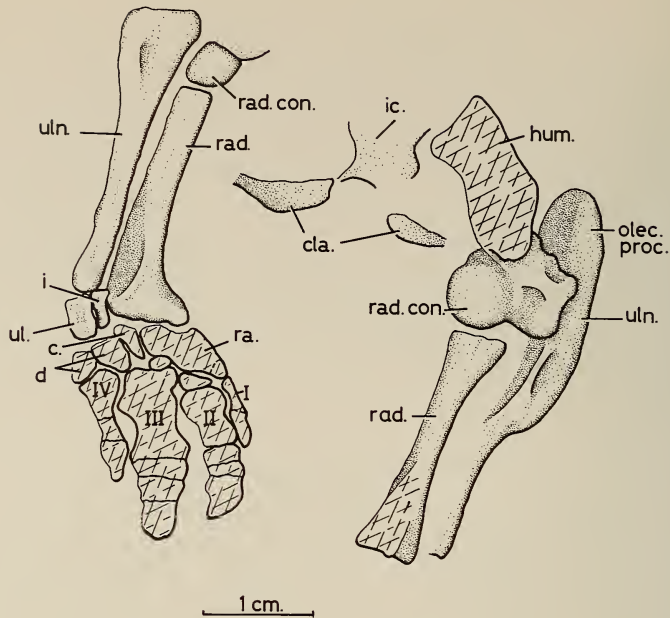


Fig. 11. *Cistecephalus* sp. BPI 2124. Left and right forelimbs as preserved. Left manus in ventral view, radius and ulna of both sides in posterior view.

metacarpal, was regarded by Brink as metacarpal V. In BPI 4120 a row of four distalia is seen.

In BPI 4120 (Fig. 12B) four metacarpals are present in the right manus, the two middle ones being the largest. These are interpreted as being, from medial to lateral, the first to fourth metacarpals; a small bone close inside the fourth metacarpal may be a reduced fifth metacarpal. Four metacarpals are present in BPI 2124 (Fig. 11), Brink's (1952) specimen, these being nos. I, II, III and IV. In BPI 696, where the carpus is very incomplete, a splint of bone alongside the fourth digit may represent a fifth metacarpal. Three metacarpals are in position in BPI 2915 (Figs. 6, 13A). These have been identified as nos. II, III and IV. A loose, damaged element lying medial to the rest of the wrist bones may possibly be a dislodged first metacarpal.

A digital formula can be obtained in GS K224, the specimen described by Keyser (1973). This is the only specimen to show a hand with five digits (Figs 12A, 13B). The left hand, seen in ventral view, is best preserved. The first digit is reduced but appears complete, with the two phalanges separated by only a narrow line of fusion. There is a small metacarpal. Digits 2 and 3 are robust, also with the first and second phalanges fused, and are provided with powerful ungual phalanges. The ungual phalanx of digit 2 is damaged but was clearly of a size comparable with that of 3. The fourth digit is reduced in size,

and about the size of the first, while the fifth is also small. Here there is an ungual phalanx smaller than that of 4, and a single phalanx is preserved behind this. The right manus is also preserved, and preparation of digit 5 shows that it is complete; it is smaller than the others but consists of an ungual phalanx and fused first and second phalanges. The digital formula of this specimen is thus 2,3,3,3,3.

Several other specimens show details of the manus. In BPI 2915 (Figs 6, 13A) three digits are present, two of them nearly complete. In two digits, regarded as the second and third, the first and second phalanges are immovably united, and can be distinguished from each other only by a thin line of fusion. Medially a third fused pair of phalanges lies separated from the radiale by a space large enough to accommodate a metacarpal; this probably represents the first digit, with the first and second phalanges fused. The ungual phalanges of the second and third digits are damaged, but that of the third digit is of

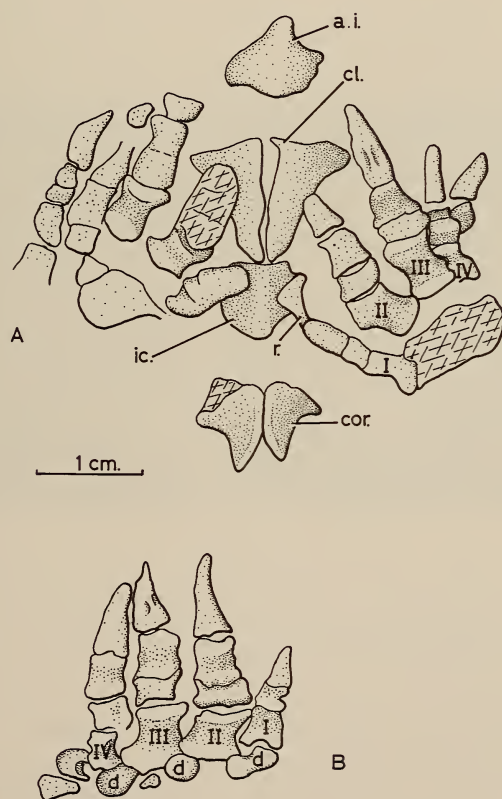
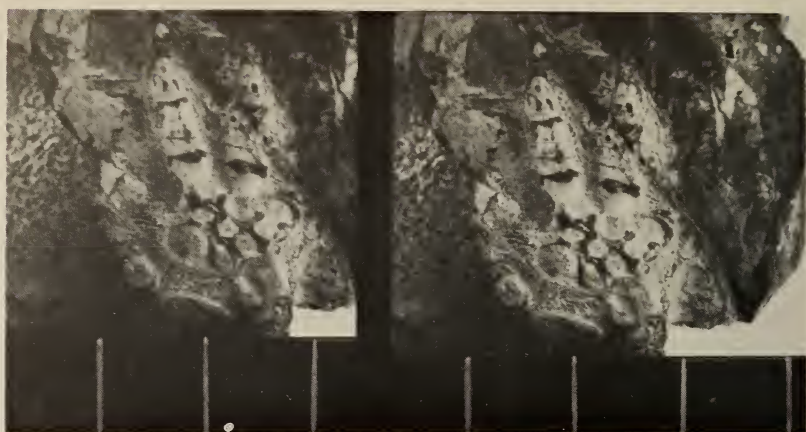
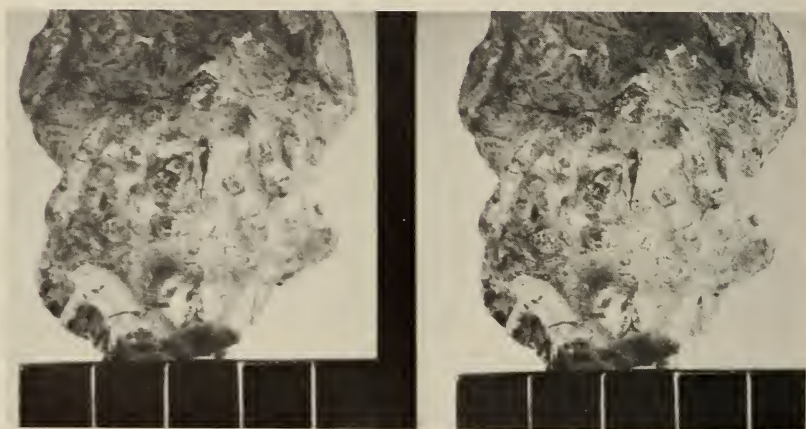


Fig. 12. *Cistecephalus* sp. A. GS K224. Left and right manus in ventral view, as preserved. B. BPI 4120. Right manus in ventral view.



A



B

Fig. 13. *Cistecephalus* sp. A. Stereophotographs of BPI 2915, left manus in ventral view. B. Stereophotograph of GS K224. Left and right manus in ventral view.

considerable length. Only a fragment of the first phalanx of the fourth digit is preserved. In BPI 4120 (Fig. 12B) four digits are present, these being the first, second, third and fourth. In all the first and second phalanges are closely united but in only the first digit have the two reached the stage of semi-fusion found in the case of BPI 2915. The ungual phalanges are long and sharp-pointed, particularly that of the second digit. In the second, third and fourth digits the

first phalanx is shortened to almost disc-like proportions. In overall appearance the manus is short, wide and powerful.

In BPI 696 a left manus, with a very incomplete wrist, is preserved. As interpreted, the first, second, third and fourth digits are present. In the first digit the first and second phalanges are fused, while in the other digits this is the condition in the first two phalanges, the ungual phalanx being movable on the distal tip of the second phalanx. In Brink's (1952) specimen, BPI 2124, a part of the first metacarpal is preserved, and possibly part of the first phalanx (Fig. 11). Digits 2 and 3 are complete, and the first two phalanges of each are firmly united and separated by a line of fusion. The fourth digit is very incomplete, but at least one phalanx is present.

The absence of a fifth digit in all but one of the specimens available is probably best regarded as being due to accidents of preservation resulting from this digit's relatively delicate structure.

Pelvic girdle and hind limb

The pelvic girdle is preserved in BPI 696 (Fig. 14B), BPI 2450 (Fig. 16B) and BPI 4086 (Figs 14A, 16A). The ilium lies well forward in relation to the other pelvic bones with the blade forming a strong anterior process. A posterior process is clearly demarcated from the base of the bone. Above the acetabulum the base of the ilium is drawn out as a buttress terminating in a laterally directed process, while in front of the acetabulum its anterior surface is broad and flat. The pubis forms the ventral part of the acetabulum and the anterior wall of the obturator foramen. Ventrally it carries a low keel set off laterally to the ventral border of the bone. The ischium forms a lower rim for the acetabular socket which is not as strongly developed as the iliac buttress. The acetabulum is shallowest on the ischium and deepest on the ilium, where the iliac buttress overhangs the socket. All three bones are firmly united and the puboischiadic plate lies at an angle to the ilium, suggesting that the two ischia approached each other in the ventral midline. There is, however, no indication of a bony or cartilaginous symphysis between the two halves of the pelvis.

In BPI 2450 two clear depressions and a third less distinct one on the inside of the iliac blade mark the points of attachment of the sacral ribs. The most anterior of these lies some way behind the anterior tip of the ilium and is shallow and fairly long. The second is deep in comparison and lies above the anterior border of the acetabulum. The third depression may mark the attachment of the last sacral; it lies close behind the preceding one. If the sacral vertebrae were held horizontally, these depressions, which lie some distance below the dorsal border of the iliac blade, show that the pelvis must have been rotated so that the puboischiadic plate lay largely behind the acetabulum.

The ilium of BPI 2450 (Fig. 16B) differs in some respects from that of BPI 696 and BPI 4096. The iliac blade is shorter than in BPI 696, and the anterior border of the anterior process is turned out laterally and descends to meet the highest point of the acetabular buttress well behind the anterior edge of the

bone. As a result, the iliac blade is laterally concave. There is no sign of a separate posterior process at the base of the ilium, but the dorsal crest of the bone does extend back a short way. In overall view, therefore, the ilium is a high, narrow bone. The acetabulum appears to be deeper than in BPI 696, and bounded by a more prominent rim; the posteroventral, ischial part of the rim is almost as strongly developed as the anterodorsal, iliac part.

The structure of the hind limb can be determined in BPI 4096 (Figs 15, 16). Both femora are preserved, the right one being the better exposed. The bone is a remarkable one, with a strongly developed head carried medial to the inner border of the shaft and standing well forward of the anterior surface of the bone. The greater trochanter is confined to the lateral corner of the proximal part of

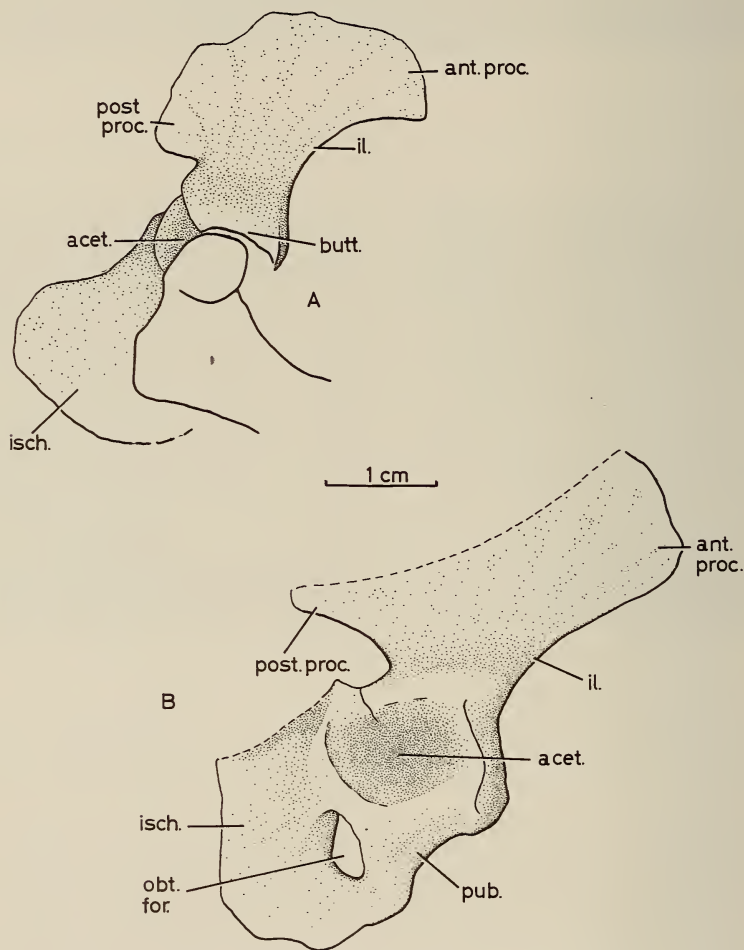


Fig. 14. *Cistecephalus* sp. Pelvic girdle in right lateral view. A. BPI 4086. B. BPI 696.

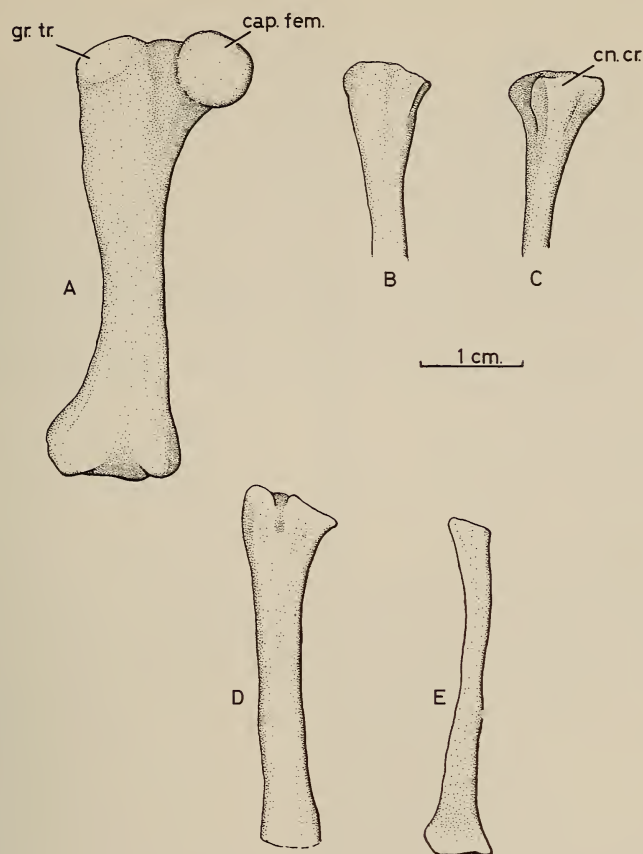


Fig. 15. *Cistecephalus* sp. BPI 4086. A. Right femur in anterior view. B. Right tibia in medial view. C. Right tibia in anterior view. D. Left tibia in lateral view. E. Left fibula in lateral view.

the bone, and does not extend down the shaft as a separate crest. The antero-posteriorly compressed shaft is slightly rounded anteriorly but almost perfectly flat behind. Distally the bone is expanded for the articular areas with the tibia and fibula. The proximal end of the bone between the head and expanded greater trochanter is essentially as narrow as the shaft.

The proximal ends of the tibia and fibula are preserved on the right side but both bones are fully exposed on the left side, except where the distal end of the tibia is partially obscured by the foot. The tibia is a well-ossified bone with the proximal articular surface roughly triangular in outline. There are two clear areas for articulation with the condyles of the femur, forming two corners of a triangle completed by an anterior cnemial crest. Proximally the lateral

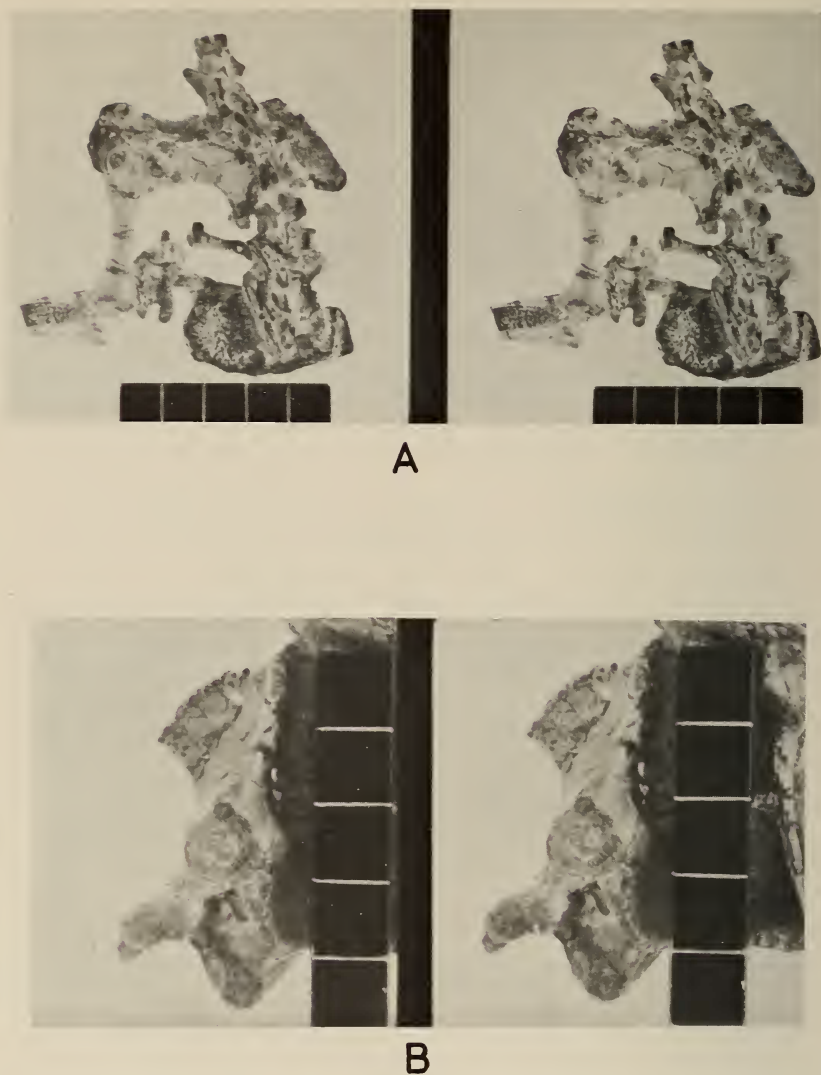


Fig. 16. *Cistecephalus* sp. A. Stereophotograph of BPI 4086. Right ilium, femur and proximal part of tibia and fibula. Left astragalo-calcaneum in proximal (dorsal) view. B. Stereophotograph of BPI 2450. Right half of pelvic girdle in lateral view.

surface of the bone bears a groove which may have received the dorsal part of the fibula (see Watson 1960). Distally the shaft becomes narrower and lateromedially compressed, but it widens again to form a rounded condyle for articulation with the tarsus.

The slender fibula is slightly expanded proximally where it lay up against the lateral side of the tibial head. It could not have had more than a small area

of articulation with the femur, but distally it widens to form a small, flat articular surface for the tarsus.

The left tarsus and pes, slightly separated from the tibia and fibula, are preserved nearly complete and are seen in ventral view (Figs 16-17). The astragalus and calcaneum appear to be unique among dicynodonts in that the two bones are united and can be distinguished from each other only by a notch and a line marking the fusion between them. Their proximal surfaces combine to form a wide, concave articular area for the tibia and fibula. The largest

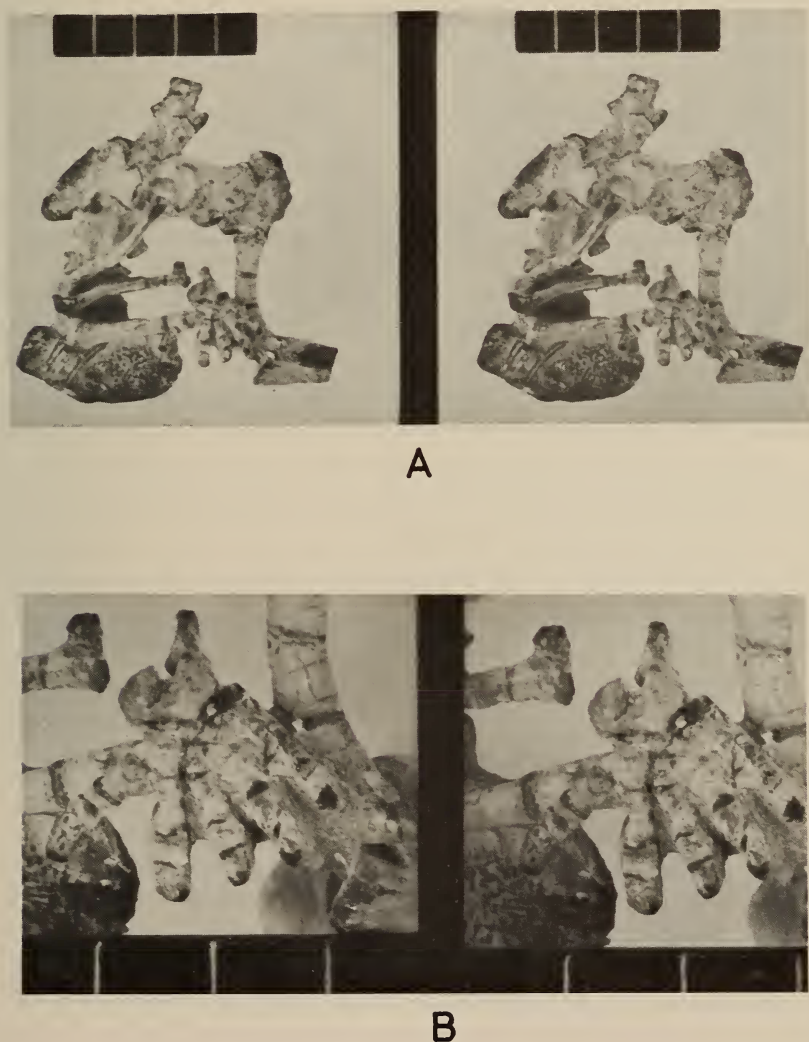


Fig. 17. *Cistecephalus* sp. BPI 4086. Stereophotographs. A. Left ilium, femur, tibia, fibula and pes. B. Left astragalus-calcaneum and pes in ventral view.

part of this surface is formed by the astragalus and is more concave than the smaller calcaneal surface which met the fairly flat distal part of the fibula. The distal surface of the calcaneum, more extensive than that of the astragalus, is rounded for its meeting with the tarsal bones. The size and strength of the structure, and its well-developed articulation with the tibia and fibula, are surprising in a reptile such as *Cistecephalus*, and suggest considerable movement at the ankle joint, including rotation between the astragalo-calcaneum and the tibia and the fibula, and flexure and extension between astragalo-calcaneum and the foot.

In front of the astragalo-calcaneum are two proximal tarsal bones, one seen only very indistinctly. These probably met the medial part of the calcaneum and the lateral part of the astragalus. Following on these is a row of four distal tarsals. The most medial of these meets the first metatarsal and part of the second metatarsal; the third meets the third metatarsal while the fourth and largest touches the base of both fourth and fifth metatarsals. The metatarsals of the second, third and fourth digits are short and fairly slender. Only in the fifth digit can three phalanges be distinguished, and these are not very clearly shown. The rest of the digits have suffered varying amounts of damage. Only two phalanges are found in the second, third and fourth digits, while in the first digit only one separate phalanx could be identified. In this digit, a small bony flake might represent part of a terminal phalanx.

RANGE OF MOVEMENTS AND MUSCULATURE OF THE LIMBS

Attempts at reconstructing musculature and limb movements in extinct reptiles, particularly in the case of forms which have no living descendants, inevitably involve some degree of speculation, but if this shortcoming is clearly borne in mind the exercise can be a useful and informative one. In the following, only general features in the bony structure and only those main muscle groups which are expected to be present in all terrestrial reptiles are considered (see Romer 1922, 1944). Cox (1972) has given a more detailed account of the musculature and possible range of movement in the forelimb of *Kawingasaurus*, where the material included separated bones which could be manipulated and where the relations between the joints could be better determined than was possible in the case of the *Cistecephalus* material available for the present study.

Pectoral girdle and forelimb

The pectoral girdle of *Cistecephalus* is unusual in several respects. The girdle as a whole lies well forward, leaving a short neck with the scapula relatively close behind the skull. The glenoid cavity faces almost straight laterally while the blade itself, instead of sloping slightly forward, is vertical or even posteriorly inclined in its upper half. The base of the scapula has rotated forward and the acromian process, rather than being a separate projection, is part of the general anterior edge of the scapular blade. The clavicle appears to have lain at an angle of approximately 45°, from an acromian connection

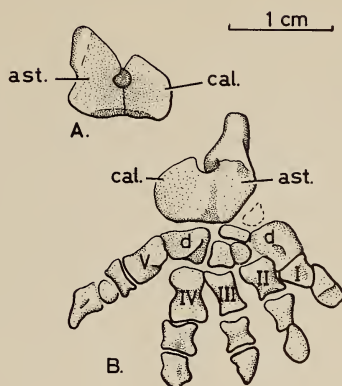


Fig. 18. *Cistecephalus* sp. BPI 4086. A. Left astragalo-calcaneum in proximal (dorsal) view.
B. Left pes in ventral view.

straight down to a second support at the anterior edge of the procoracoid. This may be associated with the forward position of the shoulder girdle as a whole relative to the vertebral column and skull. Besides being strongly braced by scapulae and procoracoids, the clavicles also meet in the ventral mid-line in an extensive face-to-face contact.

These features of the pectoral girdle can be interpreted in terms of resistance to strong lateral forces which were imposed upon the forwardly rotated glenoid region of the scapulocoracoid. Such forces would have been transmitted internally on to the clavicle which, instead of bracing the scapulocoracoid against stress from a posterolateral direction, had to support that bone against forces of almost purely lateral origin. To help counter these forces, the acromian articulation was extended dorsally so that the clavicle enjoyed an extensive dorsoventral overlap with the scapula; at the same time the ventral part of the clavicle rotated back to meet the anterior edge of the procoracoid in an extra point of support. The substantial meeting between the clavicles in the ventral mid-line may be regarded as a further strengthening device.

The relationship between the glenoid cavity and humerus is also of significance. The glenoid is a well-finished socket, with a sharp dorsal rim on the supraglenoid buttress. The humerus carries a distinct humeral head, set off as a dorsal condyle on the proximal part of the bone, and it is evident that all movement between humerus and glenoid took place about its slightly convex articular surface. With the humeral head dorsally oriented the deltopectoral crest faces forwards, and the twist of the humerus along its long axis is such that the condyles for the radius and ulna are directed forward at an approximate angle of 45° to the horizontal. With the head of the humerus facing forward in the glenoid cavity the distal condyles of the humerus face straight

down. Judging by the relations between the head of the humerus and the glenoid, this 45° rotation, accompanied by forward and back swing, was the most general movement of the upper arm.

The highly developed articulations between the radius and ulna and the humerus indicate that considerable movement between upper and lower forearm was characteristic of the animal. While the radius seems restricted to a rocking motion against the radial condyle of the humerus, the ulna is notched for articulation with the ulnar condyle and distal edge of the humerus. The depression on the humerus immediately proximal to the ulnar articulation suggests, too, that the ulna could be straightened on the upper arm by the action of muscles attaching on its high olecranon process.

Powerful extension of the forearm on the humerus, best explained as a digging or scraping movement for which the broad, powerfully constructed manus with its fused phalanges and strong claws was clearly suited, would account for the lateral forces directed on to the glenoid region of the scapulo-coracoid. A consideration of some of the chief muscles associated with the pectoral girdle and forelimb supports this interpretation.

In a dicynodont such as *Cistecephalus* it is expected that the main muscles bracing the scapula on the side of the trunk were the trapezius muscle anteriorly, inserting on the anterior edge of the bone and on the cleithrum, and the levator scapulae superficialis muscle. These arose from the posterior and posterodorsal part of the rounded occipital area of the skull and from the ligamentum nuchae. Posteriorly the scapula would have been held in position by the serratus anterior superficialis muscle, arising from the spines of the dorsal vertebrae and inserting on the dorsal edge of the scapula. The backward slope of the dorsal part of the scapula in some specimens may indicate a division of the insertional areas of these three muscles: the levator scapulae superficialis anteroventrally, the trapezius anterior anterodorsally and the serratus anterior superficialis posterodorsally.

Muscles which are generally responsible for movement of the humerus are, superficially, the latissimus dorsi, arising from the surface of the back and flank behind the pectoral girdle, and the deltoideus group, arising from the scapula and clavicle as the scapular and clavicular deltoid muscles. In *Cistecephalus* the area for insertion of the deltoideus is clearly marked off from the head and more posterior part of the humerus by a crest running from the base of the head to the ectepicondyle. The pectoralis muscle normally arises from the sternum and ribs and inserts on a process below the proximal end of the humerus. In *Cistecephalus* the insertion areas of both the deltoideus muscles, pulling the humerus forward and up, and the pectoral muscle, pulling the humerus back and down, are greatly expanded as a powerful deltopectoral crest, giving both muscle groups added leverage on the upper arm and reflecting their increased size. Another muscle important in locomotion is the sub-coracoscapularis, which arises from inside the girdle to insert near the head of the humerus and which serves to pull the humerus back—in *Cistecephalus* the

prominent medially oriented internal process marks the point of insertion of this muscle, and is evidence of its increased importance during locomotion. Cox (1972) suggests that due to the similar medial position of the internal process relative to the condyle in *Kawingasaurus*, contraction of the subcoracobrachialis would also have resulted in a downward thrust of the humerus. Other muscles inserting on the humerus would have been the scapulohumeralis anterior, arising from the forward part of the girdle and inserting near the head of the bone, and the supracoracoideus, extending from the anterior part of the coracoid plate to the underside of the humerus.

Movement of the forelimb is brought about by the triceps muscle dorsally and the biceps and brachialis muscles ventrally. In *Cistecephalus* the areas of origin of the triceps on the humerus were the posteromedially extended internal process and the expanded area behind the ectepicondyle which, as shown above, is demarcated from the deltoideus insertion area by a crest. The third triceps head arose from the scapula. In *Cistecephalus* the insertional area of the muscle, the olecranon process, is greatly enlarged over the normal dicynodont condition, and it is evident that the triceps, though short, was a muscle of considerable size and able to exert powerful extension forces on the lower arm.

Besides extension and flexion movements of the forearm on the humerus, it is likely that anteroposterior swing of the forearm was possible (see Cox 1972). Such movements would have been controlled by flexor and extensor muscles arising from the ectepicondyle and entepicondyle of the humerus; in *Cistecephalus* these are powerfully developed and extend well in front of and behind the condyles for articulation with the radius and ulna.

Seen in its entirety, the structure of the pectoral girdle and forelimb in *Cistecephalus*, characterized by strong processes for muscle attachments and well-finished joints and articulations carrying a minimum of cartilaginous lining, suggests that the animal was capable of using its forelimbs in controlled movements of considerable power. As suggested above, these movements may be interpreted as forming part of habitual digging or scraping activities.

Pelvic girdle and hind limb

In the hind limb all joints and articulations are, as in the forelimb, characterized by well-ossified and smooth bony surfaces. The relationships of the femur to the pelvic girdle and lower hind limb are of particular significance. The prominent, rounded femoral head projects medially and forward on the narrow proximal part of the bone, and it is clear that a considerable range of movement was possible at the acetabulum. The offset head suggests that the femur was held with the lower end drawn in close to the body in a mammal-like fashion, with movement taking place mainly in a vertical, parasagittal plane. In addition, the fact that much of the articular surface on the head faces forward as well as inward suggests that the femur could rotate medially along its long axis so that the anterior part of the head came to lie deeper within the acetabulum. In this position the greater trochanter on the proximolateral corner of the bone

is turned forward, while the condyles for the tibia face slightly outward, turning the lower leg away from the body. Since the condyles on the femur for articulation with the tibia face distally as well as posteriorly, it is likely that the lower limb could have been extended far forward on the femur.

The strengthened astragalo-calcaneum provided a single, large articular surface for movement between the foot and the tibia and fibula. The rounded distal end of the tibia has a radius of curvature smaller than that of the broadly concave astragalus, but the fibula terminates in a relatively flat articular surface which coincides more closely with the surface of the calcaneum. Movement between the astragalo-calcaneum and the tibia and fibula must have involved considerable rotation and even sliding between the bones of the lower limb and tarsus.

Increased rotatory movement between the lower leg and the pes could be the result of the femoral rotation discussed above, during which the lower leg was directed away from the long axis of the body. For example, if the femur were rotated inwards along its long axis while in the forward position, the lower leg could have been flexed back and away from the body in a scraping movement; however, rotation of the femur would have resulted in lateral displacement of the lower end of the tibia and fibula, and could have occurred only if compensatory movements were possible between the lower leg and pes while the pes was firmly placed on the ground. Thus, longitudinal rotation of the femur and the development of a broad articular surface on the astragalo-calcaneum in *Cistecephalus* are probably related phenomena, and are indications of unusual hind limb function in the living animal.

Although areas of muscle attachment are less clearly marked on the bones of the hind limb than on those of the forelimb, some observations can nevertheless be made regarding the possible arrangement of the hind limb musculature. In reptiles several muscles are responsible for movement of the femur. The puboischiofemoralis internus arises from the lumbar region and inner surface of the girdle and inserts on the femur near its head. In *Cistecephalus* a large, forward-facing area on the base of the ilium probably served for the origin of part of this muscle, which served to pull the femur forward. The iliofemoralis muscle in reptiles arises from the ilium and inserts on the upper surface of the femur, drawing it back; in *Cistecephalus* a distinct greater trochanter on the proximolateral corner of the bone shows that the muscle inserted in a primitive mammal-like fashion. Other muscles which generally draw the femur back are the caudifemoralis muscles arising from the tail, but the tail in *Cistecephalus* and other dicynodonts is weak and it is unlikely that these muscles were very important—no trochanter for their insertion is found on the femur. However, backward pull on the femur would have been provided by the ischiotrochantericus (obturator internus) running from the inside of the ischium to the head of the femur. In addition, an adductor femoralis arising from the pubo-ischiadic plate would have attached down the ventral surface of the femur and served to pull the leg back.

For the lower leg a group of extensor muscles, the iliotibialis and femurotibialis, run from the girdle and femur to insert on the tibia. A distinct cnemial crest on the *Cistecephalus* tibia indicates a well-developed femurotibialis, while the distally placed tibial condyles on the femur show that the lower limb could have been almost fully straightened upon the femur. Flexor muscles for the lower leg would have included the puboischiotibialis, running from the pelvic girdle to the lower leg.

The hind limb has clearly been modified in a different way to the forelimb. While the humerus has become broad and robust, with enlarged processes for the attachment of muscles, the femur is slender in comparison with other dicynodonts. The manus is relatively immobile and powerfully constructed, while the pes again is small but very mobile on the lower leg. In terms of length there are also significant differences between the bones of the forelimbs and hind limbs. Thus, the femur and tibia are both longer than their counterparts in the forelimb, the total length of the humerus and radius being approximately 73 per cent of the total length of femur and tibia. Although the point of articulation between the humerus and glenoid cavity is lower on the body than is the articulation between the almost vertically held femur and the acetabulum, it appears that the pelvic region of the body was held higher off the ground than the pectoral region during ordinary locomotion.

DISCUSSION

In its skull and jaw, axial skeleton, pectoral and pelvic girdles as well as in its appendicular skeleton, *Cistecephalus* shows a wide range of modifications which together make it probably the most aberrant of dicynodonts. It follows that *Cistecephalus* was adapted to a very distinctive mode of life, and that the general nature of the animal's habits should be indicated by these skeletal modifications. The peculiarities of the skeleton are all related to strengthening of individual bones or functionally integrated groups of bones and reflect increase in the size and power of various parts of the musculature. The clearly defined and in some cases enlarged areas of articulation between bones of the limbs and girdles, and the distinct articular condyles, with a minimum of cartilaginous capping, on the humerus and femur, all point to a high degree of muscular control over the limbs during movements of considerable power. Indications are that the forces exerted during these movements were far in excess of the requirements for normal locomotion, and it can be deduced that the limbs were frequently used during additional activities that formed an integral part of the animal's life. Moreover, the overall similarities between the skulls of *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*, and between the pectoral girdle and forelimb of *Cistecephalus* and *Kawingasaurus*, suggest that the family Cistecephalidae was adapted to a broadly uniform way of life.

Cox (1972) concluded on the basis of available material that *Kawingasaurus* was an active digger, and it is now possible to assign a similar way of life to *Cistecephalus* and, by inference, to *Cistecephaloides*. Compared with living

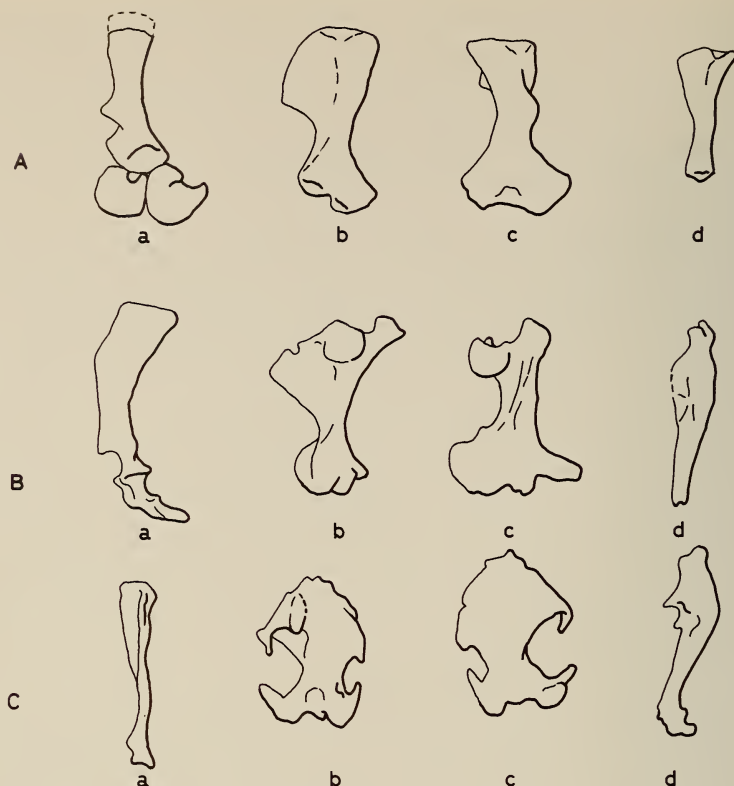


Fig. 19. Left scapulocoracoids, humeri and ulnae. Not to scale. A. *Oudenodon* sp., SAM-11114: a—scapulocoracoid in lateral view, b—dorsal view of humerus with proximal end horizontal, c—dorsal view of humerus with distal end horizontal, d—ulna in anterior view. B. *Cistecephalus* sp., from several specimens: a—scapulocoracoid in lateral view, from RC 298, b—dorsal view of humerus with proximal end horizontal, from BPI 4086 (drawn from right side), c—dorsal view of humerus with distal end horizontal, from BPI 4086 (drawn from right side), d—ulna in anterior view, from BPI 696. C. *Talpa europaea*: a—scapula in lateral view, b—humerus in posterior view, c—humerus in anterior view, d—ulna in anterior view.

mammal groups, the skeletal anatomy of *Cistecephalus* bears the closest overall resemblances with those forms which are adapted to a digging or burrowing way of life (Hisaw 1923, Yalden 1966, Reed & Turnbull 1965). Such features as a rounded occipital region, the broad humerus with powerful processes for muscle attachment, and a greatly enlarged olecranon process in *Cistecephalus* are found in analogous form in the European mole *Talpa europaea* and the Cape Golden mole *Chrysochloris asiatica* (Fig. 19). In these living forms the rounded occiput is related to increased size of the shoulder and neck muscles, while the robust humerus and high olecranon process reflect the increased power of muscles used during burrowing. The broad manus of *Ciste-*

cephalus, with three enlarged digits and fused phalanges, is suited to scraping or digging, with the highly mobile pes shovelling loosened soil to the rear and side of the animal.

The limbs and limb girdles provide the strongest evidence for digging or burrowing activities, but other features of the skeleton can also be interpreted in terms of this way of life. Thus strengthening of the skull by broadening the skull roof and eliminating the interpterygoidal vacuity in the basicranial girder, and loss of mobility between the cervical and dorsal vertebrae could indicate resistance to forces encountered by the skull and transmitted to the vertebral column during burrowing. The anterior position of the pectoral girdle relative to the vertebral column is also a feature found in both the true moles (*Talpidae*) and the Cape Golden mole (*Chrysochloridae*) (Campbell 1938, 1939) and it is significant that outward rotation of the hind limb is a characteristic of the true mole *Talpa* (Yalden 1966).

The family *Cistecephalidae*, including *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*, therefore represents a dicynodont radiation into a burrowing or fossorial way of life. Food sources such as plant roots and small invertebrates become available to animals capable of powerful digging, while the true bur-

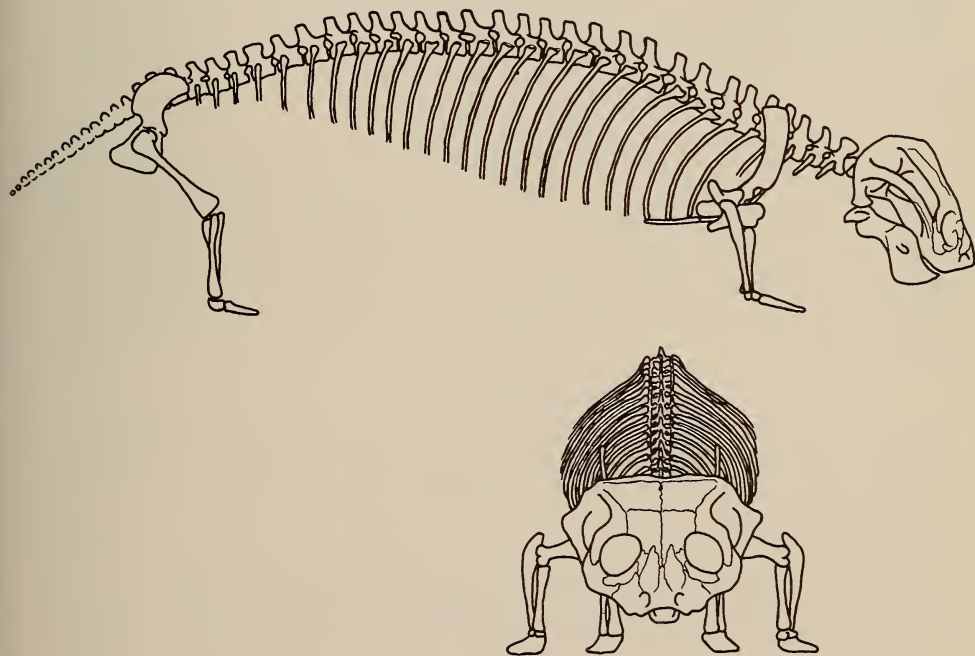


Fig. 20. Formal reconstruction of *Cistecephalus* in lateral and anterior views, mainly from BPI 4086 and SAM-10665. Approximately $\frac{3}{8}$ natural size.

rower has available an effective means of escape from predators. The degree of burrowing characteristic of the various cistecephalid genera will remain uncertain until further more definite discoveries are made; for instance, the discovery of a complete skeleton in an in-filled burrow would establish a highly-developed fossorial way of life for the particular species. Also, material at present available does not allow the actual nature of the cistecephalid burrowing activity to be identified and compared with the 'swimming' burrowing style of *Talpa* and its allies, or the 'running' style of the Chrysochloridae (Hisaw 1923, Yalden 1966, Campbell 1938). It is, however, clear at this stage that the Cistecephalidae were committed to intensification of digging or burrowing activities which probably formed only a minor part of the general way of life of other dicynodont groups.

SUMMARY

In both its cranial and postcranial skeleton *Cistecephalus* shows evidence of adaptations to a very specific mode of life. The skull is structured within the characteristic dicynodont framework, but its many substantial modifications appear to be linked with specialized features of the postcranial skeleton. Seen in its entirety, the skeleton of *Cistecephalus* represents an osteological extreme in dicynodont evolution, and all indications are that the living animal, committed as it was to at least semi-fossorial habits, was a highly unusual member of South Africa's Upper Permian fauna.

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REFERENCES

- BOONSTRA, L. D. 1966. The girdles and limbs of the Dicynodontia of the *Tapinocephalus* zone. *Ann. S. Afr. Mus.* **50**: 1-11.
- BRINK, A. S. 1950. On a new species of *Cistecephalus* Owen. *Ann. Mag. nat. Hist.* (12) **3**: 985-997.
- BRINK, A. S. 1952. Studies on Karoo reptiles. III. The manus of *Cistecephalus*. *S. Afr. J. Sci.* **49**: 13-15.
- BROILI, F. & SCHRÖDER, J. 1935. Beobachtungen an Wirbeltieren der Karoo-formation. VI. Über den Schädel von *Cistecephalus* Owen. *Sber. bayer. Akad. Wiss.* **1935**: 1-20.
- BROOM, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals*. London: Witherby.
- BROOM, R. 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Trans. R. Soc. Edinb.* **61**: 577-929.
- CAMPBELL, B. 1938. A reconsideration of the shoulder musculature of the Cape Golden mole. *J. Mammal.* **19**: 234-240.

- CAMPBELL, B. 1939. The shoulder anatomy of the moles. A study in phylogeny and adaptation. *Am. J. Anat.* **64**: 1-39.
- CLUVER, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. *Ann. S. Afr. Mus.* **56**: 155-274.
- CLUVER, M. A. 1974. The skull and mandible of a new cistecephalid dicynodont. *Ann. S. Afr. Mus.* **64**: 137-155.
- COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 321-367.
- COX, C. B. 1972. A new digging dicynodont from the Upper Permian of Tanzania. In: JOYSEY, K. A. & KEMP, T. S. eds. *Studies in vertebrate evolution*: 173-189. Edinburgh: Oliver & Boyd.
- HISAW, F. L. 1923. Observations on the burrowing habits of moles (*Scalopus aquaticus machrinoides*). *J. Mammal.* **4**: 79.
- HUENE, F. VON. 1942. Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. *Palaeontographica* **94**: 154-184.
- KEYSER, A. W. 1973. A preliminary study of the type area of the *Cistecephalus* zone of the Beaufort Series, and a revision of the anomodont family Cistecephalidae. *Mem. geol. Surv. S. Afr.* **62**: 1-71.
- OWEN, R. 1876. *Descriptive and illustrated catalogue of the fossil reptilia of South Africa in the collection of the British Museum of Natural History*. London: British Museum.
- REED, C. A. & TURNBULL, W. D. 1965. The mammalian genera *Arctoryctes* and *Cryptoryctes* from the Oligocene and Miocene of North America. *Fieldiana, Geology* **15**: 99-170.
- ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull. Am. Mus. nat. Hist.* **46**: 517-606.
- ROMER, A. S. 1944. The development of tetrapod limb musculature—the shoulder region of *Lacerta*. *J. Morph.* **74**: 1-41.
- SEELEY, H. G. 1894. Researches on the structure, organisation and classification of the fossil Reptilia. Part IX, section 1: On the Therosuchia. *Phil. Trans. R. Soc. (B)* **185**: 987-1018.
- WATSON, D. M. S. 1960. The anomodont skeleton. *Trans. zool. Soc. Lond.* **29**: 131-208.
- YALDEN, D. W. 1966. The anatomy of mole locomotion. *J. Zool. Lond.* **149**: 55-64.

ABBREVIATIONS

acet.	acetabulum
acr. proc.	acromion process
a.i.	atlas intercentrum
ant. pro.	anterior process of ilium
ast.	astragalus
at.	atlas
ax.	axis
ax. r.	axis rib
butt.	buttress of ilium
c.	centrale
cal.	calcaneum
cap. fem.	caput femoris
cap. hum.	caput humeri
cla.	clavicle
cn. cr.	cnemial crest
cor.	coracoid
cr.	crest
d.	distal carpal, tarsal
dp. cr.	deltopectoral crest
ect. con.	ectepicondyle
ent. con.	entepicondyle
ent. for.	entepicondylar foramen
fac. hum.	facet for humerus
gl.	glenoid
gr.	groove

hum.	humerus
i.	intermedium
ic.	interclavicle
il.	ilium
isch.	ischium
lat. pro.	lateral process
n.s.	neural spine
obt. for.	obturator foramen
od.	odontoid
olec. proc.	olecranon process
pa. fac.	facet for proatlas
par.	parapophysis
pi.	pisiform
pm. proc.	posteromedial process
post. proc.	posterior process of ilium
pro.	procoracoid
pro. for.	procoracoid foramen
pro. p.	procoracoid process
pub.	pubis
r.	rib
ra.	radiale
r.a.	rib articulation
rad.	radius
rad. con.	radial condyle
scap.	scapula
st.	sternum
ul.	ulnare
uln.	ulna
uln. con.	ulnar condyle
BPI	Bernard Price Institute for Palaeontological Research, Witwatersrand University, Johannesburg
GS	Geological Survey, Pretoria
RC	Rubidge Collection, Wellwood, Graaff-Reinet
SAM	South African Museum, Cape Town.